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RESPONSES OF THE LARGE WATER-STRIDER, GERRIS REMIGIS SAY, TO CONTACT AND LIGHT

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With Twelve Figures in the Text.

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I. INTRODUCTION.

Two of the most pronounced forms of behavior of many of the aquatic and semiaquatic Hexapoda are their responses to contact and to light stimuli. Study and observation of the aquatic species *Gerris remigis* Say, of the family Gerridæ, one of the common forms of aquatic Heteroptera, have demonstrated that it, also, evinces responses of this character.

Gerris remigis is a typical water-film species (Figs. 1, 11), being widely distributed in the United States on the surfaces of brooks, creeks and rivers, with currents of moderate velocity.

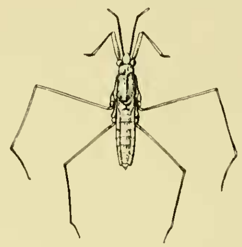

Fig. 1. The large water-strider, *Gerris remigis* Say, apterous form; a typical surface-film, stream inhabitant. Natural size. (Drawing by Beutenmüller.)

The rapidity with which it strides along the water-film, without breaking through the surface, its noticeably facile and agile movements, and the ease with which it obtains food, entangled in the surface-film, all tend to indicate the adequacy of its responses for living in a water-film habitat. Its elongated body and tapering, slender legs, spread widely apart, thus more equally distributing its weight over the water-surface, are plainly evident as this species of gerrid darts to and fro in its stream habitat. Such characteristics seem to suggest the suitableness of its bodily structure for a life on the surface of water.

II. RESPONSES TO CONTACT.

1. General Responses.

It is not uncommon for *Gerris remigis*, when striding along the surface-film to come in contact with some more or less solid body, such as a leaf, a piece of driftwood, a rock projecting above the surface of the water, the bank of the stream, or another gerrid (Figs. 2, 3, 6). Sometimes such contact does not appear to impede the movements of the insect. At other times the gerrid remains quiet for a few seconds only, while, on the other hand, there are instances when the animal keeps in contact with such surfaces for varying periods, extending from a few minutes to an hour or more. On some occasions only one leg may be in touch with the solid surface, the gerrid remaining there as if it were anchored, swaying gently with the breeze, or falling and rising with the movements of the surface of the water. Then again, one side of the body may be closely applied to some solid object, the animal staying quietly in one position, as if suddenly paralyzed. Such responses are very common in the daily life of this species and they appear to be due to its thigmotactic propensities (Figs. 2, 3).

Members of other groups of aquatic Heteroptera exhibit habitat responses to contact of a somewhat similar character to those described for *Gerris remigis*. Holmes (1907, p. 163) found that *Ranatra quadridentata* Stal. of the family Nepidæ is responsive to contact stimulation. He directs attention to the fact that:

> As a rule *Ranatra* inhabits more or less shaded retreats among submerged grass or weeds near the water's edge. It is kept in such situations, partly through the direct effect of its positive thigmotaxis, and partly because contact stimuli (as shown in a previous paper) cause it to become negatively phototactic.

According to Essenberg (1915, pp. 381-382, 383, 390), several species and genera—*Notonecta insulata* Kirby, *Notonecta undulata*, var. *charon*, *Notonecta indica*, and *Notonecta* sp.—of the family Notonectidæ are thigmotactic. She states that:

> The two pairs of forelegs are sparsely covered with hairs and are provided with claws. The latter serve for the capture of food and for attachment to the surface-film, from which they hang with their heads downward, the posterior part of the ventral surface being exposed to

the air. When in this position the fore- and middle-legs are slightly bent so that the claws are at the surface. The insects often rest at the bottom, clinging to sticks or weeds.

The contact phases of behavior of *Gerris remigis* that have been discussed are very suggestive of the responses of some other members of the Hexapoda, for example certain Agrionid nymphs, of the order Odonata, described several years ago in a paper by me (1912, pp. 274, 280), brief quotations from which follow:

In their natural habitat, Agrionid nymphs react strongly to contact. They are found clinging tightly to the stems, branches and leaves of

Fig. 2. Detail of portion of surface of brook-pool, with current passing through it—flowing to left—along margin of forested region, near White Heath, Illinois—autumn. Five water-striders, *Gerris remigis* Say, shown on surface-film in contact with solid objects and clinging to them; indicates manner of group formation. Water-striders, about one-third natural size. (For other details, see Fig. 3.) (Photograph by Lloyde and Riley.)

Elodea and *Ceratophyllum*. This is an indication of their decided thigmotactic proclivities. They tend to place as much as possible of the external parts of their bodies in contact with a solid surface. This is accomplished by clinging to the aquatic plants, in such a manner that the long axes of their bodies lie parallel to the long axes of the stems and the branches. The nymphs frequently assume a somewhat different position, with the long axes of their bodies rather oblique to the long axes of the stems and branches. The creatures are frequently found with their bodies closely applied to the *Elodea* and *Ceratophyllum* at the points where the branches are given off—that is, in the forks formed by the stem of the main plant and the lateral branches. They are also found on both plants in the angles formed by the whorls of leaves arranged around the stem.

When experiments are performed with a number of individuals in the glass trough, it is found that their movements are often very much impeded. As they swim away from the source of illumination, they frequently come in contact with the sides of the vessel and with other individuals. This contact, in many instances, impedes the movement away from the light, and causes the nymphs to become practically motionless. This is the result of the contact stimulus. They usually assume a position with the long axes of their bodies parallel with each other and in close contact, although this relation may be modified considerably. Another response, which the writer designates as the "clasping response," quickly follows. The nymphs clasp each other closely around the thorax and abdomen. The preliminary contact of their bodies causes locomotion to cease, being an example of true thigmotaxis. Then as the full surface of the body of one is applied to the body of another the "clasping response" results.

Before passing from these brief references to the writings of other observers on thigmotaxis in aquatic Heteroptera and Odonata, attention well may be directed to certain observations on the Crustacea, a less specialized class than the Hexapoda. Holmes (1903), in a very valuable and suggestive paper, has pointed out that this form of response is exhibited in a high degree by certain genera and species of the order Amphipoda, belonging to the family Orchestiidæ, of the subclass Malacostraca. Certain statements of his, with respect to two species, *Orchestia agilis* and *Allorchestes littoralis*, will be given here. He (1903, pp. 194-195) remarks that:

This instinct of *O. agilis* to get into close contact with solid objects is an expression of the strong thigmotactic tendency found among amphipods in general. It is a tendency especially marked in the aquatic representative of the Orchestiidæ, *Allorchestes littoralis*. . . . The thigmotactic reactions of amphipods keep these animals among the seaweeds and rocks where they secure protection and obtain food. The behavior of the terrestrial *O. agilis* in relation to solid objects is little modified beyond that of the aquatic species. The thigmotaxis of this form is certainly protective in function, not only by enabling the animal to escape detection by lying quiet, but by leading it into situations such as under stones or into crevices which are inaccessible to its enemies.

Fig. 3. Detail of portion of surface of brook pool, with current passing through it—flowing to left—along margin of forested region, near White Heath, Illinois—autumn. Five water-striders, *Gerris remigis* Say, shown on surface-film in contact with solid objects and clinging to them, indicating manner of response to contact stimuli, also showing beginning of group formation; during rain and wind storms gerrids take similar positions. Three water-striders shown in right background, with distal parts of legs clinging to aquatic vegetation, legs of each gerrid in contact with and overlapping those of the next one; one water-strider in left background close to rock, distal part of right middle leg in contact with blade of aquatic grass and distal part of right hind leg clinging to surface of rock; one water-strider in left foreground—slightly out of focus—head directed to left, right front and middle legs in contact with piece of driftwood. Water-striders about seven-tenths natural size. (Photograph by Lloyde and Riley.)

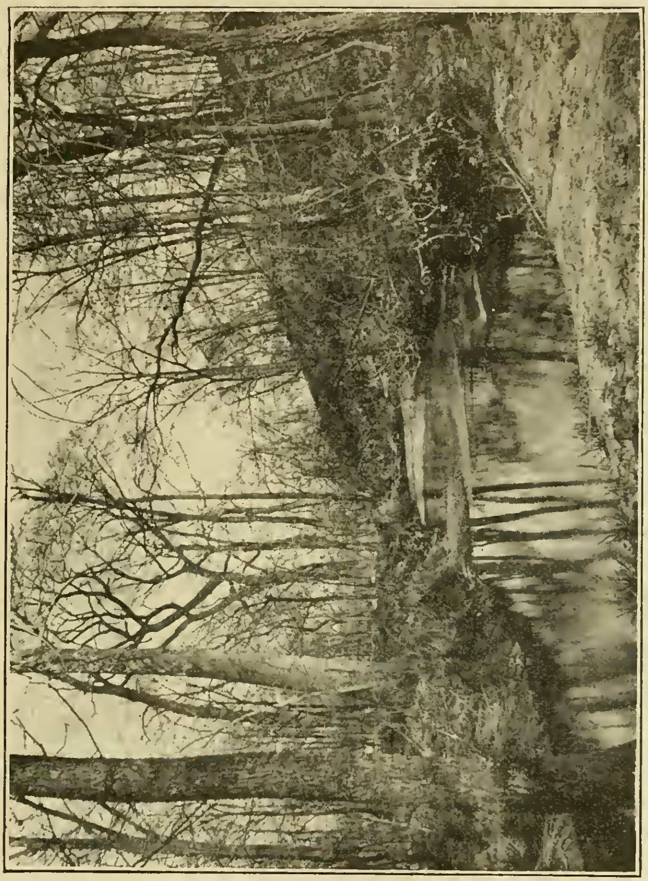

Fig. 4. Detail of Cossell Brook in Dice's Woods, a rolling, forested region—current flowing southerly, away from observer, in illustration—about one mile northwest of Charleston, Illinois—late spring. Water-striders, *Gerris remigis* Say, live on surface of such pools as indicated in foreground, frequently forming large groups on surface-film. Elms, sycamore, basswood, dogwood, hackberry, sedges, *Equisetum*, columbine, nettles, Solomon's seal, wild ginger, etc., found along the banks. (Photograph by Hankinson.)

2. Variation of Responses Under Similar Conditions.

The fact has been pointed out that although *Gerris remigis* responds to contact usually by a decrease or a cessation of its locomotory movements, yet the manner in which it responds, apparently, varies at different times. Similar facts have been observed when two or more gerrids, moving about on the surface-film, come in contact with each other, for under such conditions their responses also vary at different times. As they touch each other, the stimuli of contact may result in increased movement, the insects darting away from each other, in different directions, with great speed. This rapid locomotion may continue for several minutes before it subsides. At such times the behavior of the water-striders appears as if due to some strong or unpleasant stimuli. After the subsidence of the immediate effects of the stimuli, they continue their usual movements. In connection with the statement that the gerrids, after coming in contact with each other, may continue to stride about rapidly for sometime after contact has occurred, a quotation from Jennings (1906, p. 285) may be of interest. He states that:

> Often, of course, stimulation does rouse an organism to increased activity. But even in this case the activity is due to the release of internal energy. It may, therefore, continue long after the stimulation which inaugurated the release has ceased to act. Such continuance thus does not necessarily imply continued action of the stimulus. In many cases the specific stimulus to action is only the *change* of conditions.

The responses are not always as have been described, for on touching each other, the gerrids may not stride rapidly away, but, on the other hand, they may do so in a manner which is very slow and appears to be deliberate. Sometimes, when such contact occurs, while striding about on the water-surface, they pause for a few seconds and then move forward or backward again, usually the former movement taking place.

It is rather difficult to understand, at least from direct observation and without definite experimental evidence, why these water-striders should respond in different ways at different times, for careful and repeated observations in the field seem to indicate that they respond differently, even when the stimuli and the various physical conditions of the immediate environment remain unchanged. The natural assumption that occurs to the observer is that these different responses, to similar stimuli at different times, is due, probably, to the physiological conditions of the bodies of these insects varying at different times and, therefore, because of these differences in the physiological conditions, the gerrids do not respond in the same manner at all times to similar stimuli. Therefore, it may be assumed that the behavior of these animals is affected by the changes which occur within their bodies, and yet these changes can not take place unless there are either internal or external stimuli that bring about such changes. In this connection it is perhaps worth while to recall a brief statement by Mast (1911, p. 287):

> It is evident that such changes must be regulated by internal factors, that they must be due to alterations within the organism itself. As a matter of fact, all reactions are directly controlled by internal factors which are in turn influenced by external factors.

The general subject of "physiological states" in lower organisms has been elaborated by Jennings (1904, pp. 109-127), (1906, pp. 283-292).

3. Assembling of Groups.

Not infrequently, after coming in contact with objects protruding above the surface-film (Figs. 5, 6) the legs of the gerrids, and sometimes their bodies, become closely applied; there may be several individuals taking part in such responses (Figs. 2, 3). In this manner a number of water-striders may stop their locomotor movements and attach themselves to the group, until, eventually, a large aggregation is formed. As many as seventy-five to a hundred individuals have been enumerated in groups of this character. Usually such responses occur, not on those parts of the stream where the current is the swiftest, but rather on the surfaces of small pools, with gentle currents passing through them (Figs. 2, 3, 4, 5, 6). The gerrids may remain in such formations from a few minutes to an hour and a half, or for much longer periods. The general physical conditions of the environment, the season of the year, and the physiological conditions of the animals themselves, all these, seem to have a bearing on this matter. As viewed by the observer from a distance, such groups of insects appear as dark patches on the surface of the stream, rising and falling with the movements of the water. It was interesting to me to find in a paper by de la Torre-Bueno (1911), who is a very accurate observer, certain records of behavior of a similar character with respect to a member of the same family, Gerridæ, to which *Gerris remigis* belongs. He refers to *Metrobates hesperius* Uhler, of the tribe Halobatini, placed in the subfamily Gerrinæ. The following quotation is taken from his paper (1911, pp. 249-250):

> This is a species which, like most of the other members of the tribe, is lacustrine to a very great extent, and it may be seen congregated in large patches of blackness on the smooth waters of our lakes, or perhaps in the wide reaches of slow moving streams. It is a very active species. . . . It commonly occurs in the apterous, but the winged form seems not rare under favorable conditions.

Fig. 5. Detail of large pool at headwaters of small brook, with current flowing through it—looking down stream—near Syracuse, New York—spring. Hundreds of water-striders, *Gerris remigis* Say, form large groups on surface of pool (a), grouping themselves near overhanging banks, especially when wind is off shore; also found crawling onto and into the interstices of fallen, dead tree, separating pool into two parts, and forming groups near it. Both alate and apterous water-striders hibernate in interstices of overhanging shore (c) and among vegetation and dead leaves (b), in close proximity to pool. (Reproduced from the *American Naturalist.*)

In the early and late fall, there appears to be a much greater tendency for these groups of water-striders, *Gerris remigis*, to be formed than is the case during any other season of the year. Long and continued observations, extending over a number of years, seem to indicate that the gerrids are much more responsive to thigmotactic stimuli just previous to and while migrating onto the land to "seek" hibernation quarters, than they are under most other conditions.* Early in the fall, even on the open surface of the brook-pools, they appear to congregate more thickly and more compactly, although engaged in their usual normal responses. As the fall advances, these somewhat loose formations—more dense in appearance, however, than those of the early summer—are found nearer to the banks of the streams (Figs. 5, 6). In the late fall, large numbers of gerrids, frequently, are observed close to the land, to rocks rising above the water surface, to tree-roots extending into the water, to dams of driftwood, in fact in close proximity to such objects and places as afford them opportunity for contact, and onto which they can crawl from the surface-film. Sometimes, for days together, they are found in such situations, forming large aggregations, with their legs and not infrequently their bodies touching and the former even overlapping (Figs. 2, 3, 5, 6).

Curiously enough, strong air-currents and surface-breezes blowing along the surface-film—which in the next section of this paper are designated as agents that are active in the disintegration of groups—assist in the formation of clusters of gerrids. Such currents frequently move the water-striders nearer to each other, thus making the loose groups more compact. In addition to the mere drifting together of the insects, the winds act as stimuli that produce active responses on the part of the gerrids, for under such circumstances, they usually quickly stride close up against each other or against some solid object in the vicinity (Figs. 2, 3, 5, 6). Such stimuli not only invoke the usual contact responses, but they also induce clinging responses on the part of the insects as soon as they come in touch with their neighbors (Figs. 2, 3). Such behavior is especially noticeable when the water-striders are gathered along the leeward side of a brook or creek (Fig. 5). On the

* Data are being accumulated and experiments are being conducted with the expectation of obtaining precise evidence on this subject.

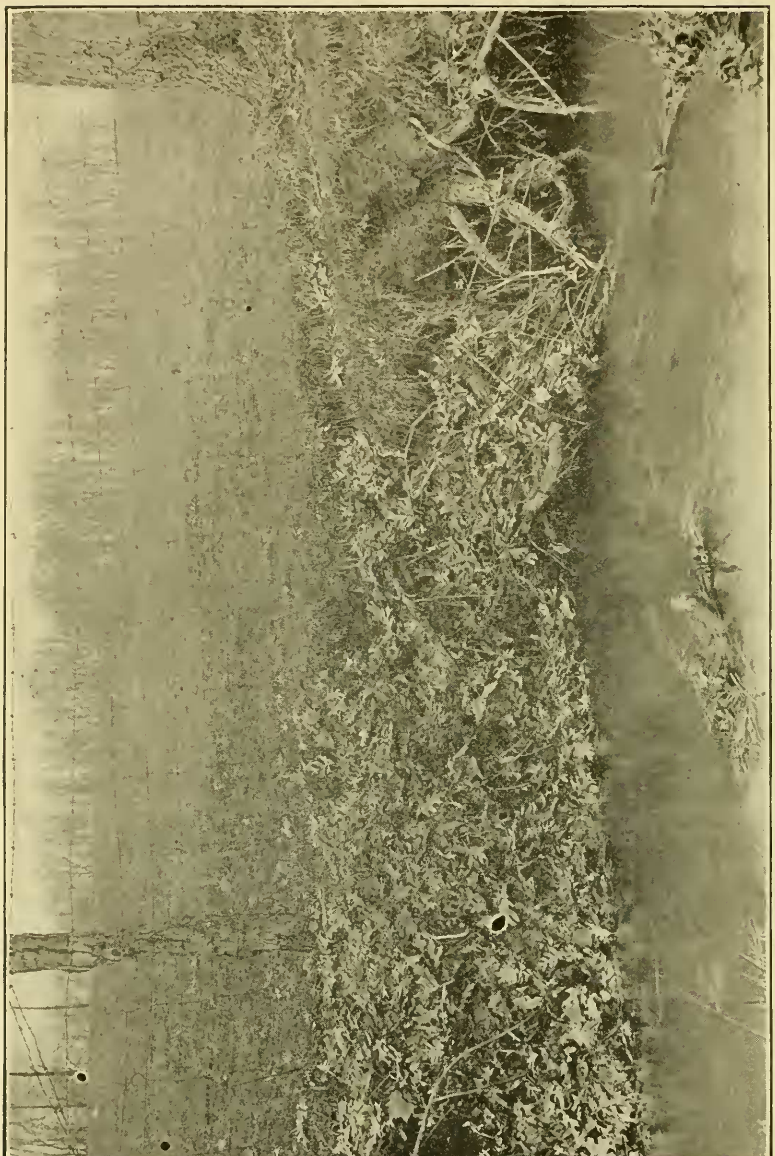

Fig. 6. Detail of bank and pool of brook—current flows to right—near White Heath, Illinois—autumn. Shows undercutting of bank, roots of tree, and clump of dead leaves—mainly oak—two to three feet in depth and six to eight feet in length; water-striders, *Gerris remigis* Say, hibernate in all three situations, frequently found in large numbers under dead leaves close to water. Gerrids often form groups, on surface-film, composed of large numbers of individuals, in contact with driftwood and dead leaves shown in center and right foreground. (Photograph by Lloyde and Riley.)

surface of a large pool (Fig. 5), near the headwaters of a small brook, in the vicinity of Syracuse, New York, and on the water-film of pools of intermittent brooks, of permanent brooks (Fig. 6), and of creeks, in the region roundabout Urbana, Illinois, such gatherings frequently have been observed. Often they were so large and the gerrids were so numerous that two to five hundred insects could be taken in less than half an hour. It should be pointed out that the best and most satisfactory evidence, for the general facts stated above, concerning the formation of groups, has been obtained in the fall. The "habit" of this species of forming groups was pointed out by me (1912, p. 281), several years ago in the following statement:

> This tendency to cluster together frequently has been observed by the writer in the case of *Gerris remigis* Say.

Other aquatic Heteroptera evince responses much like those that have been described, as Severin and Severin (1911a, pp. 100-101) have demonstrated on the part of several different species and genera. In connection with certain observations on the thigmotaxis of *Belostoma flumineum* Say, they state that:

> Again, it was not unusual to find two or more Belostomas or somewhat larger clusters clinging together at the surface or bottom of the water, a characteristic which is also noticed with *Lethocerus* (*Belostoma* aucct.) *americanum*, *Benacus griseus*, *Nepa apiculata*, *Ranatra americana*, and *Ranatra kirkaldyi*. This habit is probably a manifestation of their thigmotactic responses.

Holmes (1905, pp. 324-325) in his phototactic experiments on *Ranatra fusca*, Pal. B., of the family Nepidæ, states that:

> Efforts to go toward the light are frequently inhibited by contact stimuli. When several individuals are put into a dish of water near a window they commonly cease, after a time, to swim towards the light and form a cluster in which they lie at all possible angles to the direction of the rays.

While the experiments referred to here are related to the consideration of the subject of the inhibition of one form of response by stimuli that result in responses of another character, yet they indicate that *Ranatra fusca* also forms aggregations through the action of contact stimuli. Holmes (1905, pp. 320, 323) states that Ranatras group themselves into compact groups, in cool water, at the ends of dishes farthest from the light. In some of my own experiments (1912, pp. 279, 280), it has been observed that Agrionid nymphs, Hexapoda belonging to a totally different order, the Odonata, exhibit responses during the process of forming groups that are decidedly similar to those that have been described for *Gerris remigis*, and for that reason and also for a basis of comparison, they are mentioned here.

4. Disassociation of Groups.

It has been pointed out that water-striders gather in groups on the surfaces of streams, the legs and bodies of different individuals being in contact with each other (Figs. 2, 3). It also has been stated that these aggregations, probably, are due to the thigmotactic propensities of the animals. This thigmotaxis may be overcome, or at least it may be modified, by other stimuli, with the result that the groups of gerrids are broken up. Frequently, this occurs because of mechanical stimuli acting on them. Usually, this is brought about by the activity of certain individuals in the clusters disturbing others around them; or it may be accomplished by wind-currents, of considerable strength, blowing against the groups and thus causing some of the water-striders to disentangle themselves; while in other instances, members of the aggregations become active from the stimuli received from the agitation of the surface of the stream by water-currents. Driftwood, or a bunch of dead leaves, drifting with the current, occasionally strikes against one of these groups of gerrids and acts as the initial stimulus which results in its disintegration. Other Heteroptera exhibit similar responses, for Holmes (1905, pp. 318-325) has pointed out, in his experimental investigations on the water-scorpion, *Ranatra fusca*, that members of this species, responding to stimuli of one character, not only may have these responses modified, but also may have them inhibited through the influence of stimuli of a different character. It is interesting to notice that behavior of this general character is not limited to the Hexopoda, but that it is evinced by members of a less specialized class, the Crustacea, as Holmes (1901, p. 212) has demonstrated in his experiments on the freshwater shrimp, *Gammarus locusta*, belonging to the order Amphipoda and to the subclass Malacostraca.

Some of the gerrids in these gatherings are more active than others and thus, probably, less responsive to contact stimuli. These from time to time move their legs and bodies, in this way disturbing other water-striders next to them. Such disturbances act as mechanical stimuli on still other individuals in the groups. In this manner, whole clusters may be affected and may become disorganized, so that there is a tendency for them to disintegrate. The insects that have become the most active are most likely to leave the aggregations first. Then others in their immediate vicinity follow, so that eventually all the members of any individual aggregation free themselves from it and are found striding back and forth on the surface-film as separate units. Often the gerrids on the outside of the groups are the first to break away, but this is not always the case, for individuals crowded into the centers of the masses of water-striders have been observed to pull loose from the others in contact with them and then to stride over, or to push between, those forming the peripheral parts of the groups, until they reached the free surface-film. Generally, it appears to be more difficult for the gerrids in the centers of the clusters to free themselves, than is the case for those nearer the outer margins to do so.

With respect to the manner in which the disintegration of the aggregation of gerrids occurs, it is interesting to notice that members of a related family, Nepidæ, have been observed to evince behavior of a somewhat similar character. Holmes (1905, p. 308), writing of the responses of *Ranatra fusca*, found that individuals of this species formed groups in aquaria, and he states that:

> In this way they may lie for hours in an almost motionless state.

He (1905, p. 323) also has observed that an aggregation of this character is more likely to disintegrate as the animals exhibit more activity. Again, this writer (1905, p. 308) remarks that in these clusters, which are formed by *Ranatra fusca*, the insects

> are often so closely aggregated and so tangled together that those which are near the center of the group experience much difficulty in disengaging themselves.

Other Hexapoda display responses not dissimilar to those of *Ranatra fusca* and *Gerris remigis* in the disintegration of clusters.

Fig. 7. Detail of bunch of dead oak leaves—approximate dimensions 8 x 4 x 3 feet—on bank of brook near White Heath, Illinois—autumn. Water-striders, *Gerris remigis* Say, hibernate in large numbers under dead leaves, among tree roots—right of illustration—and in interstices of undercut bank—upper right of illustration. Leaves, forming bunches, usually in much closer contact and much more compact than indicated here and in Fig. 6. Portion of brook shown at lower right of illustration. (For other details, see Fig. 6.) (Photograph by Lloyde and Riley.)

In some of my own work (1912, pp. 283-285) on the behavior of Agrionid nymphs, of the order Odonata, it was observed that the responses exhibited, during the process of the disassociation of groups, were decidedly of a like nature to those of *Gerris remigis*. It was found that compact aggregations were formed, but that the Agrionid nymphs did not remain quiet for as long periods as either *Ranatra fusca* or *Gerris remigis* and that the breaking up of such groups was apt to occur at shorter intervals. The disassociation of these clusters resulted from mechanical stimuli and also from the activities of certain nymphs within the aggregations, although photic stimuli played a part in this process. The Agrionid nymphs in the peripheral portions of the groups were more likely to leave first, as those in the more central parts of the clusters were influenced more strongly by the contact stimuli of the individuals surrounding them, and, therefore, frequently remained more or less stationary.

5. Contact Responses and Hibernation.

During the period of hibernation, responses to contact stimuli are strongly in evidence. *Gerris remigis* begins to leave the surface-films of streams in the early autumn, continuing this migration until the late fall, and goes onto the land to "seek" winter quarters. The gerrids of this species hibernate in various situations. They have been taken from under piles of dead leaves, from interstices and deep holes in the banks of streams, from under tree-roots on the land, from under the bark in interstices of fallen dead trees, from holes in the ground under logs and driftwood, and from under piles of brush (Figs. 5, 6, 7, 8, 9, 10). They have been found, also, in such places as are mentioned by Kirkaldy (1899a, p. 151), who refers to the Gerridæ in general in the following quotation:

> As has been previously remarked, many of the Gerridæ conceal themselves—in fact "hybernate"—under moss, stones, etc., often far from water, during the winter.

However, it should be stated that, after looking through my field notes for the past few years, no records were found of *Gerris remigis* hibernating far from water (Figs. 5, 6, 7, 8, 9). Further investigation may prove that alate forms (Fig. 11) of this species sometimes hibernate in other situations than those close to their own habitats. Referring to the hibernation of *Gerris orba* Stal, a congener of *Gerris remigis*, Essenberg (1915a, p. 397) states that:

> The water-striders pass the winter as adults, hibernating under logs, rocks, rubbish, and in other sheltered places.

It is evident that these two species pass the winter in somewhat similar situations. While Hungerford (1919, p. 117) has little to say regarding the hibernation of *Gerris remigis*, the records that he does give are correct. He remarks that:

> Our large *G. remigis* winters as an adult hidden under some brush, logs or other shelter about the water.

His records are from Kansas and it is interesting to notice that he points out the fact that this species hibernates in the vicinity of its own habitat. It should be stated that *Gerris remigis* is mainly an apterous species (Fig. 1) and it is to be expected that few even of the alate forms (Fig. 11) will be found hibernating at any great distance from their aquatic habitats (Figs. 4, 5, 6, 7, 8, 9). In a paper by me (1919a, p. 484), on certain habitat responses of *Gerris remigis*, there is a brief statement of some extended observations on the hibernation of this species on and near the margin of a large pool, at the headwaters of a small, rapid stream, in the vicinity of Syracuse, New York, which is quoted here:

> They [*Gerris remigis*] undoubtedly hibernate, in large numbers, along the shores of this pool. In fact, I have found a few of them hibernating in interstices where the shore slightly overhangs the water, and also among dead leaves and other vegetation at points from a few inches to three yards away from the pool.

On several occasions, a few alate individuals (Fig. 11) have been found hibernating within three yards of the water (Fig. 5).

In all of these situations, where water-striders were found, the insects kept in close contact with their immediate surroundings and with each other. In some of these places, they have been taken in large numbers (Figs. 6, 7, 8, 9). They have been found in groups, frequently as many as fifty individuals in a cluster. Sometimes the aggregations were so large that one hundred and fifty to two hundred and fifty gerrids have been counted. Often in these winter quarters (Figs. 5, 6, 7, 8, 9, 10) they lie in close contact with each other, their bodies being closely applied. Such responses were, very probably, due to their thigmotactic propensities.

At this point it may be mentioned that a number of other entomologists have referred to the hibernation quarters of water-striders. Among these are Uhler (1884), McCook (1907), and Kellogg (1908). From the context, it is to be inferred that all three of these writers refer to *Gerris* (=*Hygrotrechus*) *remigis*. Uhler (1884, p. 268) makes the statement that:

> These insects stow themselves away under the banks of streams, in the mud beneath leaves or rubbish, or at the bottom of water under stones and roots of trees when the autumn begins to be cold, and from thence they reappear upon the surface of the water as soon as the warm weather of spring returns.

McCook (1907, p. 265), when writing about the hibernation of water-striders, remarks that:

> When winter sets in the survivors of the season burrow into the mud, or under bunches of dead leaves and withered grass-stalks or stones or other rubbish, and there lie dormant or semidormant until spring again calls them to active life.

Kellogg (1908, p. 198), in referring to the situations in which water-striders hibernate, makes the following statement:

> In late autumn the water-striders conceal themselves in the mud beneath leaves or rubbish or at the bottom of the pool under roots or stones to hibernate, coming out again with the first warm days of spring.

I wish to state that it was a long time before I found *Gerris remigis* in a hibernating condition. Search was made in almost every conceivable situation before the hibernation quarters of this species were located. Many careful searches were conducted during a large part of one winter before any hibernating individuals were discovered, and a part of a second winter passed before they were found in numbers. For a period of years, both in the autumns and in the winters, careful observations were made of the behavior of these water-striders, not only as they migrated into places of hibernation, but also after they were settled in their winter quarters (Figs. 5, 6, 7, 8, 9, 10); and I never have found them hibernating in mud, in water, at the bottom of water, at the bottom of a pool, pond, brook, creek, or river.

During the hibernating period, the gerrids evince little movement. Within a radius of two miles of White Heath, Illinois, in the months of December and January, large numbers have been taken from holes in the banks of brooks—but not

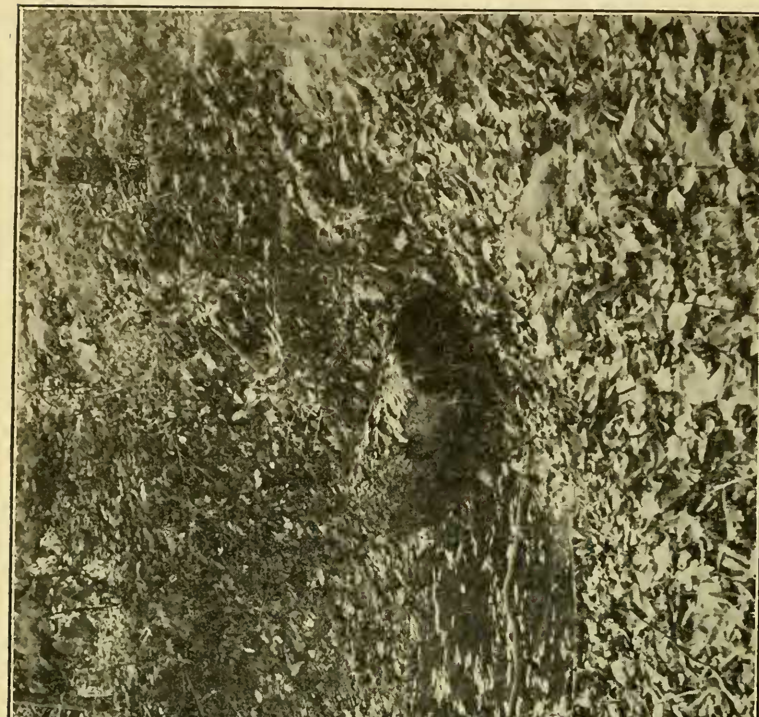

Fig. 8. Detail of small intermittent brook—during high water, current flows southeast, in illustration to left—Brownfield Woods (elm-maple deciduous forest), about three miles northeast of Urbana, Illinois—autumn. Shows drought conditions, greater part of brook being dry, except for a few small, isolated pools, three being shown in bed of brook in foreground. Water-striders, *Gerris remigis* Say, found on this brook, pass from one pool to another, over dry bed of stream, by method of trial and error; when photograph was taken, gerrids observed only on pool next to log; ten days earlier found on all three pools. Water-striders observed leaving surface-film for hibernation quarters in interstices of undercut bank, under dead leaves, under log, in interstices of and under bark. Trees, shrubs and herbaceous vegetation shown along bank of brook. (Photograph by Chenoweth.)

in mud—from holes on the land, filled in with dead leaves and drift debris left after floods, under the roots of trees, and from under compact masses of dead leaves (Figs. 5, 6, 7, 8, 9). There would be so many of them from one location that they scarcely could be held in two cupped hands. At such times it was noticed that they were very quiet, there being hardly any movement at all on the part of the gerrids. If they were taken from their winter quarters during a thaw, there was more movement than was the case during freezing weather. Occasionally, when their hibernating quarters were uncovered, the insects were almost overlooked, because they remained so quiet and in such close contact with the substratum and with each other. There was, in addition, another fact which increased the difficulty of finding them and that was the frequent similarity in color of the background to the color of the water-striders. It has been observed by me (1912, p. 275) that certain other semiaquatic Hexapoda, Agrionid nymphs of the order Odonata, exhibit somewhat similar responses.

In general it may be stated that when hibernating water-striders were found, their bodies were closely applied to each other. Those on the periphery of the group were in close contact with their immediate physical surroundings on the one side and with the gerrids forming the inner portion of the cluster on the other side. Frequently, their legs were so inextricably entangled that on lifting up a few members of the aggregation, many others would be found clinging to them. Essenberg (1915a, p. 400) has recorded responses of a similar character with respect to a closely related species of water-strider, *Gerris orba*. In connection with certain of the statements made above, a quotation from one of my own papers (1919, pp. 402-403), on some habitat responses of *Gerris remigis*, may be of interest:

> During hibernation, there is no question about water-striders remaining quietly in one place for a long period of time. But it must be recalled that the temperature is low at such times, and that they frequently seek dry situations. . . . The positive thigmotactic responses of these gerrids have been observed frequently during periods of hibernation. At such times they formed tangled masses, which were due to the water-striders crowding closely together. These facts were recorded in my field notes as early as the winter of 1912–1913.

The different phases of behavior that have been discussed, such as crawling into the various hibernating quarters which have been enumerated, the crowding together into clusters, and the motionless state in which the gerrids lie, are due in part, if not largely, to contact responses, although there have been accumulated certain facts that seem to indicate that the crawling into winter quarters may be partially the result of a tendency toward negative phototaxis at the hibernation period. However, more evidence is needed on this point.

These gerrids seem to be responsive to contact stimuli not only during the hibernation period, but also at its inception. Apparently, both the dorsal and ventral surfaces are sensitive to contact as well as the legs and lateral sides of the body. Frequently, they have been found in piles of dead leaves (Figs. 5, 6, 7, 8, 9) with their bodies in such positions as to suggest evidence for the above statement. Their bodies were in contact with a leaf above and with a leaf below, the legs being stretched out as nearly as possible in the same plane as that of the body. The legs and bodies of the insects appeared to be rigid and they were so to the touch of the fingers. It was possible to lift the body of a gerrid by means of the posterior pair of legs, without bending them, the animal remaining perfectly stiff and motionless while this was done. All of this was very suggestive of the death-feigning response—briefly discussed later in this paper—which is induced, certainly in part, by contact stimuli. The gerrids evidently had crawled into the masses of leaves through the interstices formed between the different individual leaves (Figs. 6, 7, 8, 9). Such movements brought not only the upper surface of the body in contact with the leaf or leaves above this surface, but it also brought the lower surface of the body against the leaf or leaves below this latter surface. In many instances it was clear that the spaces between the leaves were so small that the water-striders could not have walked erect into the interstices (Figs. 6, 7, 8, 9), but must have raised their legs almost to the same plane as that of the body and almost parallel with its longitudinal axis. In fact, not infrequently, individuals have been found with their appendages exactly in the position described.

However, there is considerable positive evidence with respect to the points just discussed. On several occasions the gerrids have been observed, after they had left the surface-film, walking along in a direction more or less parallel with piles of leaves situated about a yard from the bank of the stream from which the water-striders came. They have been seen to enter such masses of leaves by way of the spaces left between the individual leaves of these bunches (Figs. 6, 7, 8, 9). Sometimes they attempted to enter the masses of leaves by means of interstices between the individual leaves so small that it was impossible for them to walk in an upright position while doing so, or even after they had entered the interstices (Figs. 6, 7, 8, 9). It should be stated that, in course of time, these large bunches of leaves become very firm and compact (Figs. 6, 7, 8, 9). It was found that the insects overcame the difficulty of entrance, in some instances at least, by pressing the proximal portions of the legs so closely against their bodies that these appendages extended laterally from them and appeared to be almost in the same plane. In other instances the legs were raised until they were almost in the same plane as the bodies of the gerrids and slightly oblique from parallel to their long axes. These water-striders have been found under the bark of fallen, dead trees (Figs. 7, 8, 9) and in their interstices (Fig. 5) in spaces so restricted, that if the animals actually had not been observed to crawl therein, it would seem rather difficult to account for their presence in such situations. Often they have been taken from under heavy logs (Fig. 7, 8, 9) and driftwood, in such places where it seemed no insect could remain without being crushed. The act of crawling into locations of the various characters that have been indicated, as well as the act of staying there quietly, seems to be partially explained at least by their thigmotactic responses. There is some evidence that these gerrids may be negatively phototactic at this season; if this proves to be true, it would have to be taken into consideration in the final summing up.

6. Contact Responses and Drought.

Some extended observations made, during the years 1911-1913 inclusive, on *Gerris remigis*, with reference to certain habitat responses, present additional information on the behavior of this species to contact stimuli. These observations were concerned mainly with the responses of the gerrids after their stream habitat had become dry (Figs. 8, 12), during

Fig. 9. Detail of log, bank of brook, and pool of small, intermittent brook, showing drought conditions, Brownfield Woods, near Urbana, Illinois—autumn. Shows part of isolated, brook pool, which water-striders, *Gerris remigis* Say, inhabit. Gerrids observed to leave surface-film for hibernation quarters in interstices of undercut bank, under bunches of dead leaves—usually much more compact than indicated in illustration—under stones, under log, in interstices of and under its bark. (For other details, see Fig. 8.) (Photograph by Riley and Chenoweth.)

periods of severe and extended droughts. It was evident, if they reached another stream or pool, that the result was accomplished by means of trial and error. During the course of their wanderings, they frequently came in contact with various objects in their path, such as lumps of dry mud, driftwood, clumps of dead leaves, and stones (Figs. 8, 12). Often, the forward movement of the gerrids ceased at such contact. Stimuli of this character inhibited locomotion and the water-striders became stationary, their bodies being applied closely to such objects as have been enumerated. Apparently, as a result of such contact stimuli, sometimes they crawled underneath these obstructions (Figs. 8, 12). In both cases, whether their bodies were in close contact with the objects, or whether they crawled beneath them, they remained stationary for various periods of time. Frequently, these extended from a few minutes to an hour or more. Sometimes, after such inhibition of locomotor activities, there was a change in the direction of their movement, when their journey was renewed. Occasionally, they fell or jumped into large cracks which had been formed in the mud of the dry bed of the stream and they remained there during intervals of time extending from a few minutes to several hours, on one occasion at least for three hours. During such wanderings as occur after their habitats become dry (Figs. 8, 12), responses to contact appear to be a common feature of their behavior. Contact stimuli, frequently, result in inhibiting locomotor activities and cause the insects to become quiet, so that they remain motionless in one position for various periods of time.

7. Contact Responses and Laboratory Observations.

While conducting certain experiments in the laboratory on *Gerris remigis*, some phases of the behavior of these water-striders indicated that they responded to contact stimuli. After collecting the gerrids in the field, they were placed in large, glass aquaria—dimensions 36 x 18 x 20 inches—in the laboratory. These aquaria contained a few inches of water and several large stones, the upper surfaces of which protruded an inch or so above the surface of the water. At first the insects moved about freely on the surface of the water, but, frequently, after a few minutes of time, some of them left the water-surface and climbed up onto the surfaces of the stones. Very soon the leaders were followed by others, until, eventually, the majority of the gerrids had left the water. The entire upper surfaces of the stones were covered by the water-striders, sometimes several layers in thickness, so that they presented the appearance of dark brown masses extending above the surface of the water. The insects remained motionless, with their legs and bodies entangled in clusters. If undisturbed, they often stayed in these compact groupings for hours and even for days. The solid surfaces of the stones and the contact of the bodies of the hemipterons appeared to act as stimuli, inhibiting movements and resulting in the gerrids lying motionless for long periods of time.

Many of the insects left the surface of the water and crawled up the perpendicular glass faces of the aquaria, a response probably due to gravity. However, they did not remain in such situations, for within one or two hours they were all assembled, with the exception of a few individuals that were still leaving the surface of the water, in the angles formed by the meeting of two of the glass sides of the aquaria. Frequently, in these angles, there were formed tangled masses of gerrids, extending from a point one or two inches above the water-surface to the very tops of the aquaria. Several of the aquaria had metal flanges, extending inwards, placed at right angles to the upper edges of the upright glass sides. The juxtaposition of these flanges and the perpendicular sides of the aquaria formed right angles, and, often, many of the insects were found in these angles. Pearl (1903, pp. 560-562), experimenting with planarians, applied the name goniotaxis to responses of a similar character. The gerrids climbed to the very tops of the aquaria and formed tangled groups all round their upper edges and especially in the corners formed at the meeting points of the flanges and of two upright glass surfaces. Responses of this character were first observed when conducting experiments with some half dozen gerrids in each aquarium. It was noticed that the water-striders had disappeared. After searching for them carefully, it was found that they had crawled to the tops of the aquaria and had taken up positions such as already have been described. In a number of the aquaria, stones were placed close together, but with small spaces between them. It was observed that the gerrids crowded into these openings and came to rest there, often staying in a quiescent condition for several hours and on a few occasions for several days. In these various observations, it appeared as if the angles of the aquaria and the close proximity of the stones exerted contact stimuli to which the water-striders responded by coming to rest in such positions. In situations of this character large areas of their bodies were in close application to the substrata.

Certain members of the class Crustacea, belonging to the order Amphipoda, for example some of the species of the family Orchestiidæ, evince thigmotactic responses which are very similar to those of *Gerris remigis*. Because of this similarity, attention is directed to the careful observations made by Holmes (1903, pp. 194, 195) on three species of the Amphipoda, *Orchestia agilis*, *Allorchestes littoralis* and *Orchestia palustris*. Brief quotations from the paper by Holmes are given here:

> *O. agilis* generally continues hopping until it alights in a place where it can readily get under some object or wedge itself between bodies, so that it secures contact on a considerable surface of its body.

Writing of *Allorchestes littoralis*, he mentions how it glides away when it is disturbed and continues his remarks as follows:

> The efforts are continued until they bring the creature into some niche or crevice where the contact sought for is obtained; then it curls up and lies quiet.

With reference to *Orchestia palustris*, Holmes states that:

> The tendency to get under or between objects is as strongly developed in this species as in *agilis*, and contact has apparently a stronger quieting effect upon it. When lying quiet *O. palustris* may be poked about more or less without being aroused from its thigmotactic lethargy.

While it is true that the observations on *Gerris remigis* were made on individuals confined in aquaria and the records of Holmes were obtained in the habitats of the Amphipods, yet the responses in the two cases were so much unlike—and similar behavior on the part of the gerrids has been observed in their own environment—that a brief comparison seemed to be desirable.

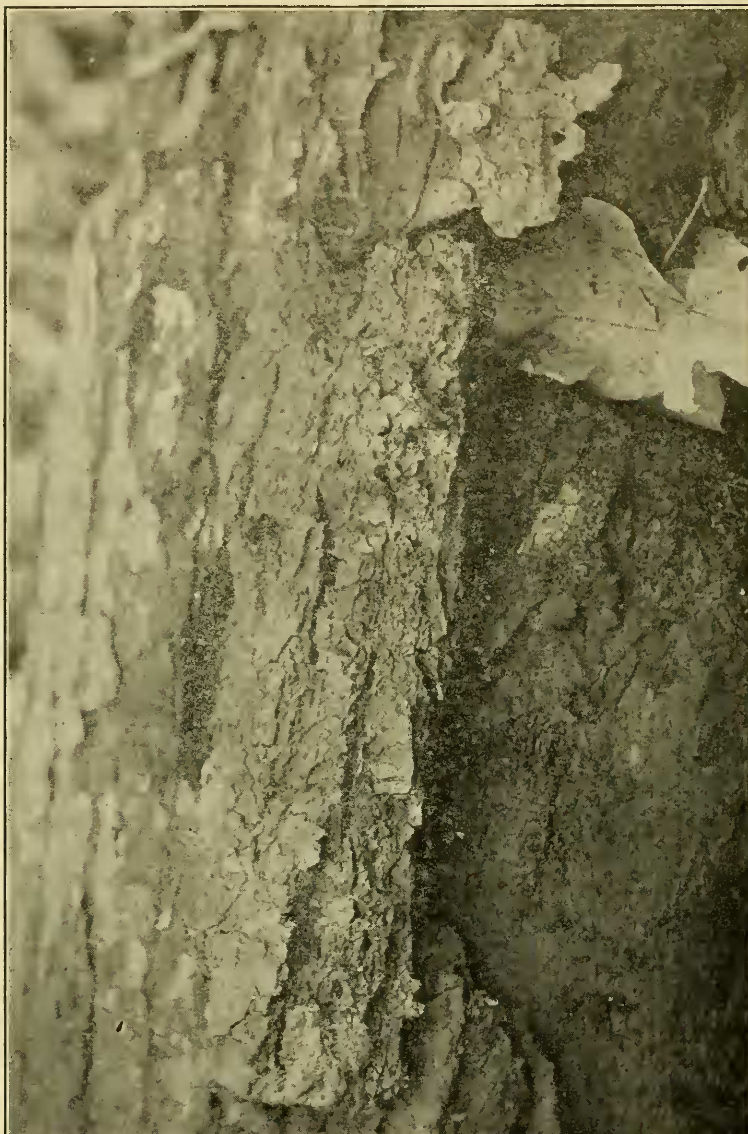

Fig. 10. Detail of log in bed of intermittent brook, Brownfield Woods, near Urbana, Illinois—autumn. Water-striders, *Gerris remigis* Say, hibernate, in large numbers, in interstices of and under bark of log, also in deep depression under leaves in foreground. (For other details, see Figs. 8, 9.) (Photograph by Riley and Chenoweth.)

8. Contact Responses and Death-Feint.

Another form of response, related to contact, often is evinced by these gerrids and that is the death-feint. This frequently can be induced by gently stroking the dorsal sides of their bodies. Sometimes, merely touching the animals is sufficient stimulation to obtain the death-feigning response. In other instances, if they are picked up in the fingers, this response occurs. However, on other occasions, it is very difficult to elicit the death-feint and sometimes, no form of contact stimuli calls forth the response. Essenberg (1915a, pp. 399-400, 402) states that *Gerris orba*, a congener of *Gerris remigis*, feigns death, the response being very pronounced in certain individuals. The response can be elicited by contact stimuli. On arousing from the death-feint, it again can be induced by means of contact stimulation. The normal position assumed by *Gerris remigis* during the death-feint is for the body to lie flat against the substratum, where it becomes rigid. At such times the front pair of legs and antennæ are stiff and stretched forward, while the middle and hind pairs of legs also become rigid and are stretched backward. The legs assume a position as nearly as possible in the same plane as that of the body and almost parallel with its longitudinal axis. The insects remain perfectly motionless during the response and may be handled without arousing them from the death-feint. They may be lifted by the posterior pairs of legs without these being bent. At such times, the entire weight of the body is supported by these legs. Often, on arousing from the death-feint, stroking the body and other forms of contact stimuli again induces the response. On the other hand, after the death-feigning response has continued for some time, contact stimuli, frequently, arouses the animals from it, as does dropping them onto the surface-film of water.

Members of other families of aquatic Heteroptera besides Gerridæ exhibit the death-feigning response, for example, the water-scorpions, *Ranatra fusca* (Holmes, 1906), *Ranatra quadridentata* (Holmes, 1907)—both of the family Nepidæ—*Belostoma flumineum* Say and *Nepa apiculata* Uhler (Severin and Severin, 1911), the former of the family Belostomidæ and the latter of the family Nepidæ. Severin and Severin (1911a) again refer to the death-feigning instinct of *Nepa apiculata*.

It is evident, from the observations and experiments of these and other writers, that responses to contact stimuli are closely associated with the death-feint. Holmes (1906, pp. 200-201, 206, 211) has pointed out the fact that contact and stroking the bodies of Ranatras with the fingers induces the death-feint. He (1906, p. 204) records the interesting observation that when the water-scorpions arouse from the response, the death-feint again can be invoked by contact. This writer (1906, p. 201) also declares that the contact of air currents brings about the death-feigning response. According to Holmes (1907, pp. 161-163), *Ranatra quadridentata* exhibits the death-feigning response. He found that the response is not so pronounced in young Ranatras as is the case in older individuals. Contact stimulation appears to be influential in eliciting the response both in the immature and adult insects. Under certain conditions, as the water-scorpions arouse from the death-feint, it can be induced again by contact stimuli.

In the interesting monograph by Severin and Severin (1911, p. 2), the fact is pointed out that *Belostoma flumineum* feigns death "when raked or scooped out of the water." Picking it "out of the water from an aquarium," or repeated contact of the fingers to the abdomen, often elicits the death-feigning response. *Nepa apiculata* readily feigns death, while in the water, if it is touched on the dorsal side "with a pencil or other object." A similar response is obtained by removing the insect from the water by means of a pair of forceps. The result is the same, whether it is grasped by the body, the breathing tube, or the legs. It is evident, in these instances, that contact stimulation is the factor which induces the death-feint. These writers (1911, pp. 6, 7) direct attention to other examples of the influence of contact stimuli in eliciting the death-feigning response. *Nepa apiculata* will feign death when placed on its back. After arousing from the death-feint it attempts to turn over onto its ventral side and in making such an attempt the animal often falls again onto its back. The effect of the shock, in falling back again, may result in inducing the response. When righting itself, the "shock effect" of dropping onto its ventral surface is frequently sufficient to elicit the death-feint. A feigning *Belostoma flumineum* can be aroused by a breath of air blowing against it. The contact of a pair of forceps, a house-fly, or another *Belostoma*, any one of these, may stimulate the animal so that it arouses from the death-feint. Then again, this species may arouse from the feint without any visible external stimulation.

Severin and Severin (1911, pp. 8, 9) state that the legs or parts of the legs of a feigning *Nepa apiculata* may be cut off without disturbing the animal. During the death-feint, this species may be cut through the prothorax and both parts of the body will remain quiet. But a feigning insect immediately arouses when dropped onto the surface-film of water. These

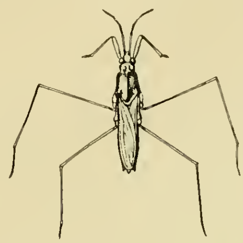

Fig. 11. The large water-strider, *Gerris remigis* Say, alate form; a typical surface-film, running water inhabitant. Natural size. (Drawing by Beutenmüller).

investigators (1911, p. 13) remark, with reference to ten individual *Nepa apiculata*, that:

> Every specimen was made to feign by taking it out of the water with a pair of forceps, dropping it upon a moist blotter from a small height and turning it over and over laterally three or four times.

In another connection they (1911, p. 16) state that:

> The death feint of Belostomas often ends suddenly when the insects are thrown into water; frequently, however, the bugs bob up to the surface of the water and continue to feign there.

With reference to the death-feint of *Nepa apiculata*, mentioned by these writers (1911a, p. 100) in the second of their papers, there is the statement that:

> When raked out of the water, together with the mud and partially decayed vegetation, these insects usually feign death, in which condition they readily escape detection, as their flat bodies are effectively concealed by the black mud and decaying plant tissue.

Regarding the origin of the death-feigning response, Severin and Severin (1911, pp. 37-38) make the following statement:

Among the aquatic Hemiptera, the death feint may have arisen out of positively thigmotactic propensities which are manifested to such a marked degree by various members of the families Belostomidæ and Nepidæ. In a previous paper, attention has already been called to the fact that *Belostoma* and *Nepa* as well as other closely related aquatic Hemiptera cluster together to form groups whenever possible, which probably is a manifestation of their positively thigmotactic response. *Belostoma* will crawl, whenever possible, beneath aquatic plants or other objects and will then often assume that death-feigning attitude in which the legs are folded against the ventral surface of the body. Specimens, which had cuddled within thick masses of *Elodea* or *Ceratophyllum*, often required a considerable amount of shaking to bring them out of their inert state. *Nepa* can be caused to feign while in water by a mere contact stimulus.

The death-feigning response is a common phase of behavior among certain Crustacea, especially among members of the order Amphipoda, of the family Orchestiidæ. Holmes (1903) discovered that both *Talorchestia longicornis* and *Orchestia agilis* exhibit this response, the latter in a lesser degree. He (1903, pp. 192-193) draws attention to the fact that, in the case of *Talorchestia longicornis*, contact with the fingers and with solid objects such as sand and small stones induce the death-feint. When the bodies of these animals are surrounded with the objects mentioned, thus giving greater contact, the duration of the response is much longer than that of individuals lying on a flat surface. As members of this species arouse from the death-feint, pressure or contact cause them to resume death-feigning. Regarding *Orchestia agilis*, this observer (1903, pp. 194, 195) states that contact stimuli exercise "a sort of hypnotic effect" on it. On the other hand, contact may arouse the animal from this condition. The thigmotactic responses of *Orchestia agilis* do not appear to be so definitely of the death-feigning character as do those of *Talorchestia longicornis*.

The entire paper of Holmes (1903) is of an extremely important character. His discussion of the probable method of evolution of the death-feigning instinct and of its probable origin are both very suggestive. He (1903, p. 195) refers to another species of amphipod, *Orchestia palustris*, of the family Orchestiidæ, pointing out that, although it responds definitely to contact stimuli and lies very quiet when in contact with and between solid objects and is aroused with difficulty from "its thigmotactic lethargy," yet its response with the death-feint is less pronounced than that of *Talorchestia longicornis*. However, its thigmotactic responses are much better developed than are those of *Orchestia agilis*. Holmes (1903, pp. 195-196) states that:

> The conduct of this species [*Orchestia palustris*] is intermediate between the thigmotactic response of *agilis* and the death-feigning of *Talorchestia*. Some specimens might almost be said to possess a death-feigning instinct.

He believes that if certain of its thigmotactic responses were

> carried out in a more decided manner and persisted in longer [that they] would result in what would commonly be called feigning death.

Continuing his discussion of the probable development of thigmotaxis into the death-feigning instinct,he remarks that:

> The death-feigning instinct of *Talorchestia* is an instinct which, I believe, has its root in the thigmotactic responses common among other amphipods. One may easily conceive that by the selection generation after generation of those individuals of *O. agilis* in which the thigmotaxis is most persistent . . . a mode of behavior like the death-feigning instinct of *Talorchestia* might readily be produced.
>
> It seems not improbable that an instinct having its phyletic root in a simple thigmotactic response may in course of time come to be comparatively independent of contact stimuli. The persistence of death-feigning in *Talorchestia* depends far less upon contact than the thigmotactic reactions of the aquatic Amphipoda, although, as has been pointed out above, contact still increases the duration of the feint.

Holmes points out that eventually contact stimulation may become necessary only to initiate the death-feigning response, but may not be required for the continuation of the feint. In course of time a mere tap or jar is all that is required to bring about the response. He points out that the death-feint is generally evoked as a response to some sort of contact stimulation. These references to the work of Holmes will be closed by directing attention to one other statement recorded by this writer. He (1903, p. 193) states that:

> *Talorchestia* does not feign death upon receiving purely visual impressions; it requires contact of some sort to elicit this form of response. The same fact seems to be quite general in the death-feigning of animals, especially below the vertebrates, and it is a circumstance, I believe, of considerable significance in relation to our views of the genesis of this instinct.

Fig. 12. Detail of part of Stony Creek, a branch of Salt Fork, a tributary of Vermilion River—showing drought conditions—near Muncie, about eighteen miles east of Urbana, Illinois—late autumn. Stream flows through a forested region. Light-colored rock in bed of creek is limestone; aquatic grasses and sedges shown in partially dry bed of stream. This part of creek consists mainly, of isolated pools, with some running water flowing to right in left background; one large pool in left background, a portion of a smaller one in left foreground, and others—not clearly shown—among vegetation in bed of creek. Water-striders, *Gerris remigis* Say, live on surface of creek and pools; gerrids become trapped in pools and, as these become dry, pass overland to other pools by method of trial and error. High clay bluff in background forms north bank of creek. (Photograph by Lloyde and Riley.)

9. Contact Responses and Rain Storms.

These water-striders frequently display a form of behavior that is at least associated with the contact response. During heavy rains, it has been found, in observations of their behavior on the surfaces of brooks and creeks, that they stride along the surface-film to the shore, to rocks, to dams formed of driftwood, and also to vegetation (Figs. 2, 3). On one of the earlier occasions when responses of this character were noticed, work was being carried on along the course of a small brook, in the vicinity of White Heath, near Urbana, Illinois. A sudden thunder shower came up and it was observed, as the rain began to fall, that the gerrids quickly left the open situations on the surface of the brook. Many of them sought the windward bank of the brook, at points where it overhung the water. Here they were found close in to the shore, usually, with the middle and hind legs on one side of the body anchoring them to the solid substratum. Others "sought" the windward sides of rocks where they attached themselves in a similar manner. In a few cases, it was noticed that they climbed up the perpendicular sides of the rocks and crept into crevices. In some other instances, they crawled up onto the upper surfaces of flat stones that were just a few inches above the surface of the water. Others came in contact with aquatic and semiaquatic plants that either extended above the surface of the water, or else grew along the margins of the brook (Figs. 2, 3). In this connection it may be of interest to direct attention to a statement by Essenberg (1915a, p. 398), made with respect to *Gerris orba*, who remarks that:

> When disturbed while on the water, the insects betake themselves quickly to the land or among the weeds, and hide by clinging to the lower surface of the leaves or by lying quietly on the ground.

Near the location where my work was being done on that particular day, there was a large dam formed of driftwood, so situated that during this storm one side of it was to windward. It was found that the gerrids were congregated here by the hundreds. Many of them were on the surface-film with their middle and posterior pairs of legs of one side placed on a portion of the driftwood. Such a position anchored them from the storm and gave them security from the wind and rain. Some left the water and crawled a few inches onto the driftwood, where they were secure. Their legs were spread out and their bodies flattened against the substratum. In a number of instances, they crept into slight depressions and interstices in the driftwood and lay there motionless. It should be stated that the great majority of the gerrids did not leave the surface of the water and those that did do so occupied positions seldom more than a few inches away from it. Those individuals, that were caught by the wind and rain on the surface-film in situations considerably nearer to the leeward than to the windward side of the brook, in the main "sought" the bank on the former side. It was noticed that a larger number of these crawled from the surface-film onto some solid substratum than was the case of gerrids on the windward side of the brook. During such storms, none or only a few of the gerrids may leave the surface-film, but always they are found anchored to, or in contact with some solid object, or else on the surface of the water in some unusually well protected situation. In this connection a statement by de la Torre-Bueno (1917a, p. 296), with respect to a related species, *Gerris marginatus* Say, is of interest. He remarks that:

> Unlike its larger congener *remigis*, it is a dweller in still waters by preference. Here at times it gathers in large numbers. In strong winds it hugs the shore, particularly if it blows that way.

After the storm was over and the sun emerged, many of the water-striders promptly "sought" the surface-film and continued their usual forms of behavior. Others delayed making this movement for several minutes after the cessation of the rain. While still others were found in contact with some solid substance for a half an hour after the storm had ended. Many of those, which first moved onto the open areas of the stream, were gerrids that did not crawl upon any solid surface away from the water. The animals which crept into depressions and interstices, in the main, were the last to reach the surface-film, probably due to the fact that greater areas of their bodies were applied to the substratum and, therefore, contact stimuli influenced them more strongly than the others which did not have such large surfaces of their bodies in contact with some solid surface. Contact stimuli appear to play a considerable role in responses of the character that have been described. Certainly they seem to have a decided effect in the cessation of the locomotor activities of the water-striders. Such stimuli not only appear to exert influence in bringing the gerrids to rest against some solid object, but also in their action in keeping them there for considerable periods of time.

III. RESPONSES TO LIGHT.

1. Habitat Responses to Sunlight.

The responses of *Gerris remigis* to photic stimuli have not yet been worked out fully. Groups of these gerrids, in their habitats on the surfaces of brooks and creeks, frequently have been observed to assemble in the shade of the banks, of overhanging rocks, and of trees. These aggregations are evident especially during the heated days of summer. Such gatherings are very common on the surfaces of streams in the prairie regions of Illinois, where, during the late summer, there is often a very high temperature and glaring sunlight untempered by any wind. On cloudless days, with the temperature at 100° F., the unshaded portions of streams frequently were entirely free from water-striders, but they were found on those parts of such waters that were shaded by trees, shrubs and other vegetation. Occasionally, there were days of this character when no gerrids could be seen on the open surface of a brook, but often on reaching some situation where the water practically was concealed by overhanging willows, alders and herbaceous vegetation, it was found, when such vegetation was disturbed, that the water-striders darted out from under it in many different directions. Hungerford (1919, p. 116), writing of *Gerris remigis* in Kansas, states that:

> They are gregarious fellows, seeking a resting place in the shade of overhanging bank or bush, but taking wildly to the open when alarmed.

However, this "seeking" of shaded situations may be the result of a combination of responses to the sunlight and to the heat, or it may be entirely a response to the latter form of stimulation. Although this needs to be tested in detail experimentally,* yet certain statements by de la Torre-Bueno (1911, p. 246) seem to suggest that temperature is a factor in influencing these gerrids to congregate in shaded situations. This observer remarks that:

> It [*Gerris remigis*] is to be found most frequently on running waters, although it also frequents still, but to a less extent. . . . They con-

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* Some experimental evidence already has been obtained and further experiments are under way. It is hoped that the results obtained will be published in a later paper.

gregate in groups in shady, slow-moving parts of streams, at the tree roots projecting from banks into the water, in the shadow of bridges, and in general in almost any place where they have some shelter from the burning rays of the summer sun.

Again referring to *Gerris remigis*, he (1917, p. 201) makes the following statement in connection with some of their habitat responses:

These beasties are common and familiar sights to the lover of the quiet flowing waters running to the distant sea. In these haunts, in some still bay or moveless backwater, under a bridge, or in the shadow of a tree, or in the cool recesses of an overhanging bank, you may see *remigis* gathered in numbers, rowing silently about. . . . Here they rear large families and spend at ease the sultry dog-days.

2. Responses to Sunlight and Laboratory Observations.

Although the habitat responses of the gerrids, referred to in the previous section of this paper, eventually may be proved to be responses to temperature rather than to light—sunlight—nevertheless, there is some positive evidence in connection with their behavior with respect to sunlight. During the summer, numbers of *Gerris remigis* frequently have been kept in the laboratory in large aquaria, of the kind already described. On several different occasions, it was observed that when a strong beam of sunlight entered an aquarium, containing gerrids of this species, that they were found congregated at the end of the receptacle farther away from the entering beam of light. Sometimes they did not crowd to the end of the aquarium, but simply moved out of the sunlight into the more shaded parts of the vessel. One afternoon, two aquaria accidently were left on a laboratory table near a window, in such a position that they were practically parallel to each other. The aquarium next to the window was almost full of water, while the one farther away from the window contained only a few inches of water. There were gerrids in both aquaria and in each case they were congregated at the end farther from the beam of sunlight that passed through both aquaria. Such behavior suggested that the water-striders were responding to the sunlight, but there remained the possibility that the response might be due to temperature, at least on the part of the gerrids in the aquarium next to the window. However, the behavior of the insects in the farther receptacle seemed to be the result of a negative response to sunlight, for it is evident that the water in the aquarium near the window must have modified to a considerable degree the temperature of the sunlight as it passed through the farther receptacle.

3. Responses to Artificial Light of Moderate Intensity.

In order to discover whether the gerrids would respond to artificial light of a weaker intensity than sunlight, the animals were subjected to electric light. They were placed in an aquarium—all aquaria used in this work being of the dimensions previously given—with parallel glass sides and ends, containing a few inches of water. The bulb of an incandescent light was hung in front of one end of the aquarium and about four inches away from it, the illumination within the field of experimentation being approximately 44 ca. m. All experiments with artificial light were performed in a dark room.

When the light first was placed near the aquarium, the insects, about fifty of them, were found to be scattered about on the surface-film. There were movements of the antennæ, legs and bodies as soon as the animals were subjected to the influence of the light. In a few seconds, perhaps half of the gerrids so oriented themselves that their heads were directed toward the source of illumination. This placed the longitudinal axes of their bodies parallel with the sides of the aquarium and also parallel with many of the rays of light passing through the bulb. It can not be said, however, that the long axes of the bodies of the insects were definitely parallel with all the rays of light passing into the aquarium from the source of illumination. Directly after orientation, the gerrids strode along the surface-film to the end of the vessel next to the light. The majority of them remained there, with their heads pointing toward the light.

By the time that these twenty-five water-striders reached the positive end of the aquarium, all but four of the remaining gerrids were oriented, with their heads directed toward the light and the long axes of their bodies placed parallel with many of the incoming rays. They then moved over the surface-film in the direction of the source of illumination, remaining at the end of the aquarium next to the light. None of the water-striders evinced a total indifference to the light, for even those that did not stride to the positive end of the aquarium, exhibited some sort of response. In certain instances there were movements of the antennæ, of the legs, or of the bodies. In other instances two or three of these sets of movements were observed. Two out of the four gerrids oriented themselves with their heads directed toward the source of light and they moved a few inches in the direction of the positive end of the aquarium. On the part of the two remaining insects, there was no orientation with respect to the light, but there were such movements of the legs, antennæ and bodies as already have been mentioned.

When the light was placed at the opposite end of the aquarium, the resulting responses of the gerrids were similar to those that have been described. The animals oriented with their heads toward the light and moved to the end of the vessel next to the source of illumination. Many individuals strode over the surface-film to the light very rapidly, the photic stimuli, apparently, exerting its influence on them immediately. By moving the light first to one end of the aquarium and then to the other, the gerrids were made to respond by moving to that end of the receptacle where the light temporarily was placed. Such experiments were performed many times with similar results. It is evident that *Gerris remigis* responds positively to photic stimuli from an incandescent light, with a field of illumination of 44 ca. m.

It has been pointed out previously that the majority of the members of this species are apterous (Fig. 1), but that occasionally a few alate forms are found (Fig. 11). In the various experiments performed up to the present time, it has not been possible to make the gerrids leave the surface of the water and fly toward the light. However, it is probable that, under certain favorable conditions, they would do so. In a former paper by me (1920a, pp. 4-5), attention was directed to the fact that a related species, *Gerris marginatus*, has been observed to migrate by flight during moonlight nights, a probable response to photic stimuli. Drought may have some bearing on such flights, as they were noticed in an interval of extended dry weather. Attention is directed to a quotation from the paper just referred to:

> On perhaps three occasions, when droughts of this character extended into the fall, I have witnessed the flight of a few isolated specimens [of *Gerris marginatus*]. I wish to state that it was several years, after I first became interested in the family Gerridæ, before I saw a water-strider fly without some artificial stimulation. Flight occurs at dusk and during moonlight nights. This fact I observed for the first time in Illinois. Flight may take place at other times also, but it has not been seen by me.

Essenberg (1915a, p. 400) has observed the flight of another closely related species, *Gerris orba*, in response to stimuli from artificial light. She states that:

> *Gerris remigis* [orba] is positively phototactic. If it takes to its wings once in a while it always flies toward the light, producing a buzzing sound as it flies.

4. Responses to Artificial Light of Weaker Intensity.

These water-striders respond not only to the stimuli of an electric light of 44 ca. m. in the field of experimentation, but they also respond to photic stimuli from a light of much less intensity. An electric incandescent light bulb, which gave 22 ca. m. illumination in the experimental field, was hung at one end of the aquarium containing the gerrids. The general responses of the animals, with respect to the photic stimuli, were noted. When the light was flashed onto them, the majority so oriented themselves that their heads pointed toward the source of illumination and the long axes of their bodies were parallel with the sides of the aquarium and with many of the incoming rays. There were thirty water-striders in the receptacle. Twenty-two responded by striding over the surface-film to the positive end of the aquarium. Most of them congregated there, but they did not remain stationary. Some crawled up the perpendicular glass end; others remained with their heads directed toward the light; while still others moved back and forth at the lighted end of the aquarium. A number of similar experiments were performed and the results, with certain slight modifications, were much the same as those that have been described.

Although no quantitative data were obtained, the general behavior of the water-striders, with respect to the source of illumination, was very similar to that recorded in connection with their responses to the electric light of 44 ca. m. in the field of experimentation. If there was any difference of importance, it was that the gerrids appeared to respond with somewhat less promptness to the stimuli of the weaker light than they did to those of the stronger illumination. According to Essenberg (1915a, p. 400) who observed the light responses of a closely allied species, *Gerris orba*, she found that:

> It is more phototactic in strong light . . . less so in a weaker light.

5. Responses to Oscillating Artificial Light of Moderate Intensity.

Not only does *Gerris remigis* respond positively to a stationary electric light, but it also responds to a moving electric light. In these experiments the source of stimulation was an incandescent electric light of 44 ca. m. in the field of experimentation. The gerrids were placed on the surface-film in an aquarium of the usual kind, containing water a few inches in depth. The bulb of the electric light was hung directly in front of one end of the aquarium and made to oscillate as a pendulum, its plane of motion being parallel to the end of the receptacle.

Thirty gerrids were used in the experiments. When the light was set in motion, the majority of the insects oriented with their heads pointing in the direction of the source of illumination. Then they moved promptly across the surface-film toward the positive end of the aquarium, in much the same manner as they did with respect to the stationary light of equal intensity. While no quantitative results were obtained, it was evident that the responses of the water-striders were more prompt with regard to the oscillating light than was the case with respect to the stationary one. They seemed to orient themselves to the source of illumination and also to move toward it more readily, perhaps, than was observed to be the case in their responses to the stationary light.

After reaching a point in the aquarium approximately eight to ten inches away from the glass end, nearest the source of illumination, the majority of the water-striders changed their direction of movement. Instead of continuing in lines practically parallel to the sides of the aquarium, they assumed positions with the long axes of their bodies oblique to the longitudinal axis of the receptacle. While their heads continued to be directed toward the general source of illumination, that is, toward the end of the aquarium where the light was placed, they now strode along the surface-film in oblique directions. Some of them turned their heads to the right and others turned them to the left. The directions in which their heads were pointed apparently depended on the swinging of the light—that is to say, it depended on the point that the light had reached in its oscillation. There appeared to be a certain amount of "indecision" as to the directions that the gerrids would take in their locomotor movements. As the light swung to the right, they tended to turn to the right and often moved for a short distance in that direction; then, as the light swung back again to the left, there was a tendency for them also to move back again in that direction. Whether the gerrids moved to the left or to the right, with respect to the oscillating light—while there were some slight movements toward it—the bulb swung back toward them so quickly that, in many instances, there were not many actual locomotor movements in its direction. So that the insects, in some cases at least, remained, approximately, in the same locations, although there were certain slight changes in positions.

Some of the gerrids congregated at the end of the aquarium nearest to the oscillating light, but they were found at any point along this end. Evidently, there was not much additional stimulation, in so far as the oscillating light was concerned, for they did not stride after it, but rather they moved about anywhere close to the lighted end of the aquarium. A few remained more or less stationary with respect to locomotion, some of them being actively engaged in cleaning their legs and antennæ. Other gerrids—as they strode across the water-film from the negative toward the positive end of the aquarium—on reaching the region where their paths became oblique, due to the influence of the oscillating light, moved close up to the glass in the end of the vessel. After the light swung past them, they moved, for a very short distance, along paths parallel to the end of the aquarium, but in the direction that the light had gone. Then, as it swung back and passed them again, some oriented themselves with their heads toward the light and moved for short distances in its direction along lines parallel with the end of the aquarium. In many instances—as the light swung past the gerrids—orientation toward the source of illumination was attempted, but this was not completed before the light was well on its way back again toward them. On such occasions, the water-striders did not orient, but continued along the paths that they already had taken. It is evident, therefore, that there was a tendency for those gerrids, which had reached the glass end of the aquarium, to follow after the oscillating light and so to move, frequently for distances of one or two inches, back and forth in lines roughly parallel with the end of the aquarium.

6. Responses to Oscillating Artificial Light of Weaker Intensity.

Experiments were conducted with the view of discovering the character of the behavior of these water-striders when subjected to the stimuli of an oscillating artificial light of lesser intensity than 44 ca. m. in the experimental field. For this purpose, an incandescent electric light of 22 ca. m. in the field of experimentation was suspended in front of the glass end of an aquarium. Then, the light was made to oscillate as a pendulum in a plane parallel with the end of the receptacle.

There were twenty gerrids on the surface of the water. When the light first was flashed onto the insects, it appeared as if all of them responded by so orienting their bodies that the long axes were parallel with the sides of the aquarium and their heads were pointed toward the source of illumination, but this soon was observed not to be the case. Five of them did not orient in this manner and fifteen of them did assume such positions as have been mentioned. Fifteen individuals responded positively to the light by striding along the surface-film toward the source of illumination. Five of the gerrids remained behind and did not move toward the light. Two out of the five responded by turning their heads toward the positive end of the aquarium, but they did not move in the direction of the light. The other three appeared to be rather indifferent with reference to the directive influence of the photic stimuli. The fifteen water-striders which had responded by moving toward the light, assembled at the positive end of the vessel. After an interval of a few minutes, the light was removed to the opposite end of the receptacle and the gerrids responded to the photic stimulation in a similar manner as before. By placing the oscillating bulb first at one extremity of the vessel and then, after a short interval of time, at the other extremity of the aquarium, the greater number of the water-striders always moved toward the source of illumination.

As the hemipterons strode along the water-film toward the light, the long axes of their bodies were approximately parallel with the sides of the aquarium and also with many of the entering rays of light, but by no means were their bodies parallel with all the incoming rays. However, when the animals reached points roughly six or eight inches from the positive end of the aquarium, their directions of locomotion became oblique with respect to the paths that they so far had travelled. Evidently these changes of directions of movement were due to the directive influence of the swinging light as it assumed various positions along the plane of its oscillation.

The further responses of the gerrids were much like those described in the experiments with the swinging 44 ca. m. electric light. The locomotor movements, in connection with the experiments with the light of weaker intensity, in a general way, were very similar to those evinced in the experiments with the stronger light of 44 ca. m. in the field of experimentation. There was, perhaps, a little less promptness in orienting to the oscillating light and also a little less definiteness in moving toward it than was the case when the light of greater intensity was employed as the source of illumination.

7. Responses to Moving but Non-oscillating Artificial Light of Moderate Intensity.

It was found that the gerrids responded readily to a moving incandescent electric light that was not oscillating. The light that was employed in the experiments was approximately 44 ca. m. in the experimental field. At the beginning of the experimental work, the light was placed directly in front of the aquarium containing the water-striders and at one end. Water was poured into the vessel to a depth of about four inches.

Contact responses modified the phototaxis to some degree, due to the fact that a large number of gerrids were used in each trial, forty to be exact.

When the experiments began, the animals were scattered about at various points on the surface-film. On the light being flashed into the aquarium, those gerrids which did not have their heads directed toward the lighted end of the aquarium, with four exceptions, immediately turned until they were standing with their heads oriented toward the source of illumination and with the longitudinal axes of their bodies parallel with the long axis of the aquarium and also parallel with many of the rays emerging from the electric light bulb. The majority of them promptly strode toward the light and congregated at the positive end of the vessel. Others paused a few seconds before they moved toward the source of illumination. Seven appeared to be indifferent to the photic stimuli, in so far as locomotion toward the light was concerned. They moved about on the surface-film apparently without any reference to the source of illumination; or they remained almost stationary; or they were busy cleaning their legs and antennæ. A majority of the seven, during the locomotor movements, kept nearer to the negative than they did to the positive end of the aquarium. This suggested, perhaps, a tendency toward being negative in their responses with respect to the light. However, while conducting several other experiments, of a similar character, it was noticed that just about as many individuals were near the positive as there were near the negative end of the vessel. These experiments showed that the larger number of the insects responded positively to the light and in much the same manner as was found to be the case in many former instances.

After these preliminary trials and after similar responses to the above had been noted in a number of different trials, the gerrids were subjected to the influence of a moving light. It was moved slowly around the outside of the aquarium close to the glass sides and ends. The majority of the insects followed after the light. Some kept just behind it, or almost parallel with it—that is, opposite to the light—while others followed at a considerable distance behind the electric bulb. In a number of instances, gerrids followed the light, but kept at a distance of four to six inches behind it. However, there was very little regularity about this. In the manner described, many of the water-striders followed the light entirely around the aquarium, until the starting point was reached. There appeared to be no difference in the responses whether the light was moved round the aquarium from left to right or vice versa. When the light was moved about above the gerrids, there was a tendency for them to keep in the lighted area. In general, the water-striders displayed considerable promptness in responding to the moving light, for they followed it with great readiness.

8. Responses to Moving but Non-oscillating Artificial Light of Weaker Intensity.

Some experiments were performed in which a moving but non-oscillating electric light was employed, in the field of experimentation the illumination being about 22 ca. m. The responses of the gerrids were of much the same character as those that have been described in connection with their behavior toward a moving light of 44 ca. m. When the light was placed at one end of the aquarium, the insects responded by striding across the surface-film toward the source of illumination. Then the light was moved slowly around the outside of the aquarium and the gerrids responded by following after it. There were no marked differences in their behavior to light of this intensity from that which they evinced in their responses to the 44 ca. m. moving light, except that it fairly may be said that they did not respond with quite the equal readiness to the photic stimuli of weaker intensity.

9. Records of Other Observers on the Phototaxis of Gerridæ and Related Aquatic Heteroptera.

Other observers have noticed that certain Heteroptera evince behavior of a definite character with respect to the photic stimuli of a moving light. Holmes (1905), in an excellent paper, has proved that *Ranatra fusca* exhibits decided positive phototaxis to a moving light and also to a light that often is changed in its position. He (1907, pp. 160-161) further has demonstrated that, in water, *Ranatra quadridentata* responds promptly to the change in position of the light. Individuals of this species respond to a moving light by exhibiting movements of the head toward it. *Gerris orba*, according to Essenberg (1915a, p. 402), responds quickly to a moving object or to a shadow. As early as the summer of 1911, it was observed by me (1920, p. 70) that *Gerris remigis* evinces responses to moving objects and shadows. Some years later, the behavior of this species with respect to a moving incandescent light of 44 ca. m. in the experimental field was noticed. The following quotation gives my statement:

> I observed, as early as the summer of 1911, that these water-striders [*Gerris remigis*] respond to moving objects and shadows more promptly than they do to stationary ones. In the early fall of 1918, I discovered that individuals of *Gerris remigis*, confined in an aquarium, respond definitely and in a pronounced manner to a moving incandescent electric light and also to frequent changes in the position of such a light.

It is very probable that photic responses form an important part of the general behavior of the family Gerridæ. Therefore, at this point it is, perhaps, worth while to draw attention briefly to some of the records of various writers on this group. Statements by Kirkaldy (1898, p. 110) indicate that *Gerris thoracicus* Schumn, in Hungary and *Gerris tristan* Kirk., in Ceylon are both positively phototactic at night. Weiss (1914, p. 33), in certain experiments with water-striders, *Gerris marginatus*, a species related to and frequently observed in similar situations as *Gerris remigis*, found that, when they were removed from the surface of a large pond and placed on the ground at distances of one to nine yards from their habitat, they returned to the water promptly. It is quite possible that vision was the most important factor in guiding these insects back again to the water. The pool referred to by this observer covered an area of 3,000 square feet and would therefore serve as an effective reflective surface. According to Essenberg (1915a, p. 400), *Gerris orba*, a species closely related to and sometimes mistaken for *Gerris remigis*, exhibits positive phototaxis, sometimes leaving the surface of the water and flying to the light. Several years ago, while conducting an extended series of observations and experiments on some habitat responses of *Gerris remigis*, certain phases of the behavior of this species indicated that vision played a not inconsiderable rôle. In this connection reference is suggested to some of my former papers (1919, pp. 410-414), (1919a, pp. 503-505), (1920, pp. 68-70, 71-72, 77-80), (1920a, p. 9). It was suggested by me (1919a, p. 499) that *Gerris marginatus*, another common species of water-strider, during migration by flight, probably finds bodies of water through the sense of sight. It should be remembered that the surface of water is an effective reflector, and large bodies of water, such as ponds and lakes, are likely to attract migrating gerrids.

Other aquatic bugs, besides members of the family Gerridæ, belonging to a number of different genera of the order Heteroptera, exhibit responses to photic stimuli. It is of interest to notice that behavior of this character is not limited to a few groups, but, on the other hand, shows itself in many more or less divergent forms. It is not the intention to make an exhaustive enumeration of the genera and species that evince such responses, but rather to point out that these responses are a phase of behavior that should receive consideration in the study of the bionomics of this order of the Hexapoda.

Comstock and Comstock (1895, p. 132) state that members of the family Belostomidæ respond to the stimuli from electric lights. Certain members of this group are apparently positively phototactic. From the context it is to be inferred that these observers probably refer to several genera of this family. It is well known, through the admirable investigations of Holmes (1905), that *Ranatra fusca* evinces positive phototaxis and that it is very strongly influenced by light. This paper by Holmes is an extremely suggestive and valuable one and for this reason it should be read carefully by all workers in animal behavior who are interested in the photic responses of aquatic Heteroptera. Because of its importance, certain quotations have been taken from it. Holmes (1905, p. 315) points out that:

> Light seems to dominate entirely this creature's behavior when the phototactic reactions are once started. It does not manifest any fear or awareness of any object in its environment save the light which it so strenuously seeks. Its excitement increases the longer it is operated with. . . .

Ranatra fusca does not always exhibit positive responses to light. Under certain conditions it becomes negatively phototactic. Holmes (1905, p. 317) makes the important statement that:

> The negative reaction is associated with a condition of lowered phototonus. It is rarely shown except when the animal is in a condition of comparative sluggishness. When in great excitement, when its movements take place with quickness and vigor, *Ranatra* always shows a positive reaction.

He (1905, pp. 318-325) has recorded a number of other very singular facts with respect to the negative responses to light. This water-scorpion may become negative in its behavior toward photic stimuli through the agency of contact stimulation, but, strange to relate, the negative responses also may be held in check by the latter form of stimuli. Further, negative phototaxis can be induced by long exposure to strong light. In another interesting paper, Holmes (1907, pp. 160-161) directs attention to the fact that the young of *Ranatra quadridentata* respond to light. In this connection, he states that:

> The reactions of young Ranatras to light are not nearly so vigorous and decided as those of the adult. A feeble positive phototaxis is manifested the first day after hatching and increases gradually as the insect grows older. Individuals a week old are very often found swimming on the side of the dish towards the light; if the dish is turned about they quickly swim again to the light side. When out of the water they are comparatively irresponsive to light—a fact in marked contrast to the behavior of the mature insects.

According to this writer (1907, p. 163), *Ranatra linearis*, a European species, is positively phototactic and occasionally flies to lights during the night. Cole (1907, pp. 382-383) has not only substantiated a number of the experiments of Holmes, but in addition he (1907, p. 397) has shown that *Ranatra fusca* can discriminate between two lighted areas that are of different size, although the illuminated fields are of the same intensity. His experiments evidently prove that *Ranatra fusca* also is able to form images of "considerable definiteness." De la Torre-Bueno (1914) has written a paper on phototropism, which is of value not only because of the discussions in it on the phototaxis of Heteroptera, but also because of the relations of these discussions to the light responses of aquatic Heteroptera in general.

Many of the species of the family Notonectidæ are responsive to photic stimuli as Essenberg (1915) has demonstrated. *Notonecta insulata* Kirby, *Notonecta undulata* var. charon, *Notonecta indica*, and a species that was not identified were all used, apparently, in Essenberg's experiments. Notonectas evince a strong positive phototaxis (1915, pp. 385-386) to various kinds and intensities of lights. The positive photic responses are intensified by increases in temperature and increases in light intensities (1915, pp. 387-388). A suggestive paper by Parshley (1917) is valuable because of its probable bearing on the phototaxis of aquatic Heteroptera. In one of my former papers (1919a, pp. 499-500), it has been pointed out that some of the genera in the family Belostomidæ are positively phototactic at night to electric lights—street arc lights. *Benacus griseus* and *Lethocerus americanus* have been observed in great numbers flying around electric street lights. It is very probable that other aquatic genera and species of the order Heteroptera exhibit phototactic responses. A recent paper by de la Torre-Bueno (1920)—and the references contained therein—is suggestive because of the explanations it may offer regarding light responses of certain aquatic Heteroptera.

IV. SUMMARY AND CONCLUSION.

1. Introduction.

This paper treats of some of the general responses of the large water-strider, *Gerris remigis* Say, one of the common species of aquatic Heteroptera, to contact and also to photic stimuli. According to de la Torre-Bueno (1911), its systematic position is as a member of the family Gerridæ, subfamily Gerrinæ, tribe Gerrini, and subgenus Aquarius Schell (=*Hygrotrechus* Stal).

The optimum habitat of the species is, in the main, on the water-films of permanent brooks and creeks, of medium size, with currents of moderate velocity. The structural characters of the body, as well as the general behavior of the species appeaı to be suited for a life in such a habitat. The species is mainly an apterous one.

2. Discussion.

Gerris remigis readily responds to contact, various objects, in its habitat, such as a piece of driftwood, a rock, a drifting leaf, and the bank of the stream serving as stimuli. Thigmotaxis is evinced by the members of this species coming to rest against such solid bodies. Contact between two individuals frequently results in a cessation of locomotion of both gerrids. Animals under the influence of contact stimulation remain stationary from a few minutes to an hour or more.

These gerrids respond to contact in a different manner on different occasions to similar stimuli, although the general conditions are not changed. When two of them come in contact with each other, they may become stationary; they may move apart slowly; or they may dart rapidly away from each other. These variations in responses probably are due to the differences in the internal conditions of the animals at different times.

Through the influence of contact, groups of various sizes are formed. The animals respond by remaining quietly on the surface-film, with their legs overlapping and their bodies closely applied to each other. These aggregations may originate near some solid object, extending above the surface of the water, or they may arise through various individuals impinging against each other. Surface breezes assist in the formation of these assemblages. The physical conditions of the environment, the physiological states of the gerrids, and the season of the year, all seem to have a bearing on this matter. Such groupings appear to be more common in the fall than is the case at any other season. They are larger and more compact at this time. The groups may consist of a few gerrids, as many as seventy-five to a hundred, or even more. Such aggregations are formed on the surfaces of pools, through which pass gentle currents, but usually they are not formed on the swiftest water, and they appear as dark patches on the surface-film. They may continue to exist from a few minutes to an hour and a half or for longer periods.

The disintegration of the groups of gerrids appear to occur mainly through the modification or inhibition of thigmotaxis by means of other stimuli. Mechanical stimulation appears to have the greatest influence in this process. This is due, frequently, to the activities of certain individuals within the groups. Their activities disturb other gerrids in the immediate vicinity and eventually result in the disassociation of the groups. Those gerrids near the peripheries of the groups generally leave first. It is usually more difficult for the individuals within the groups, near the centers, to break loose from the clusters. Very strong wind currents; agitation of the surface by means of water-currents; objects drifting with the stream, such as dead leaves and driftwood; all these seem to have much the same sort of influence in disintegrating the groups of assembled gerrids.

Responses to contact stimuli are strongly in evidence at the inception of and during the hibernation period. These gerrids hibernate in many different situations, for example, under masses of dead leaves, in holes in the banks of streams, under tree roots, under the bark of fallen dead trees, under logs and driftwood, and under piles of brush. The acts of crawling into and remaining in such places are evidently due to the contact stimuli that impinge on them at such times. They usually hibernate in large groups or clusters, sometimes as many as two hundred and fifty gerrids being found in such assemblages, although they are taken in smaller numbers. On such occasions, they are in close contact with each other, their legs and bodies being closely applied. They remain very quiet, with their bodies in close contact with the substratum. At such times, the bodies of the gerrids appear to be very sensitive to contact stimuli. They hibernate in close proximity to their own habitat.

During severe droughts, the water in the habitat of these gerrids may disappear entirely. At such times they migrate from their dry habitat, often along the beds of streams. During such migrations, they frequently come in contact with various objects, such as stones, driftwood, clumps of dead leaves, and lumps of dry mud. Their thigmotactic propensities are in evidence at such times, for contact stimuli influence the gerrids to come to rest against and underneath these objects. They also jump into cracks in the dry beds of streams. Stimulation of this sort inhibits locomotor activities, and the responses of the animals to such stimuli influence them to remain quietly in these places, with their bodies closely applied to the objects with which they are in contact. Such thigmotactic responses keep the gerrids in places of this character from a few minutes to an hour or more and even for longer periods.

In laboratory aquaria the gerrids frequently leave the surface-film and crawl onto the sides and upper surfaces of stones, extending above the surface of the water, often covering the stones several layers in thickness. They remain motionless in clusters for long periods of time. They crawl up the glass walls of the aquaria into the angles formed by the sides of the aquaria and also into the angles formed by the flanges and sides of the aquaria. They move into small spaces between stones, often staying there in a quiet condition for several days. These responses evidently are due to the thigmotactic proclivities of the gerrids. The tendency to congregate in compact masses is pronounced.

The so-called death-feigning response can be induced in these animals by means of contact stimuli. Touching their bodies or stroking them, often is sufficient stimulation to incite the response. In some instances the gerrids can not be induced to feign death through the agency of contact stimulation. The bodies are rigid and the antennæ and the legs are stiff while the response continues, the gerrids remaining motionless. At such times, contact stimuli may not arouse them from the death-feint, while on other occasions, such stimulation does so in a few seconds. Then again, there are instances, as the animals arouse from the death-feint, when the application of contact stimuli reincites the response. Vision appears to have little influence in bringing about the death-feigning response, but contact seems to be the principal factor in inducing it.

During rain and wind storms, these water-striders leave the open, exposed surfaces of streams. They are found with their bodies in close contact with solid objects, such as rocks, vegetation, banks of streams, and dams of driftwood. Usually, they are observed on the windward side of the objects that have been enumerated. If they are nearer to the leeward than to the windward side of a stream, during a wind or rain storm, they, generally, move to the former side. Frequently, they crawled from the surface-film onto these objects, many of them moving into crevices. Sometimes, they congregated by the hundred in such situations as have been mentioned, their bodies being in close contact with the substrata. Evidently, these responses are due to the thigmotactic proclivities of the animals. After the abatement of a storm, they again moved onto the surface-film. Some, promptly, "sought" the surface of the water, others after a few minutes delay, while still others did not reach the water-surface for a half an hour after the storm had ceased. Many of those that moved onto the surface-film last came from depressions and interstices in the substrata. Probably, they were influenced more strongly by contact stimuli than was the case of the other gerrids. Contact stimulation plays a definite part in such responses, exerting an influence to bring the gerrids to rest against solid bodies and also in keeping them in such situations for considerable periods of time.

Gerris remigis readily responds to photic stimuli of various intensities. Frequently, on cloudless days, at a temperature of 100° F., they are not found on the open, unshaded surfaces of streams. They congregate in the shade of the banks, rocks, trees, and other vegetation. However, this may be partially due to responses to temperature and may not be due entirely to negative responses to strong sunlight.

In laboratory aquaria, they are found to be, on certain occasions at least, negatively phototactic to sunlight. They move, either to the ends of the aquaria farthest from the beams of sunlight, or else they simply stride out of the sunlight into the more shaded regions of the aquaria.

The majority of these gerrids are positively phototactic to electric light of 44 ca. m. within the field of experimentation. In an aquarium, when fifty individuals were used, they orient with their heads pointing toward the source of illumination, thus having the longitudinal axes of their bodies parallel with many of the entering rays. Then, they stride to the positive end of the vessel. When the light is changed to the opposite end of the aquarium, the gerrids respond again by moving toward the source of illumination. All of them do not orient to the light with equal promptness. Some delay for several seconds before completing this response. None appeared to be entirely indifferent to the light. A few individuals moved only two or three inches toward the source of illumination. A few others evinced movements of the antennæ, legs and bodies. Sometimes, there were one or two alate individuals among those subjected to photic stimulation, but none of them flew toward the light.

Water-striders respond positively to the stimuli of an electric light of 22 ca. m. in the field of experimentation. Their behavior with respect to light of this intensity is much the same as that described for a light of 44 ca. m. in the field of experimentation. The chief differences of importance are that the gerrids neither orient quite so promptly to, nor do they move so readily toward the light of lesser intensity.

Gerris remigis responds positively to an oscillating electric light of 44 ca. m. in the experimental field. The light oscillated in a plane parallel to the end of the aquarium containing the gerrids. Thirty water-striders were used in the experiments, the majority of them orienting with their heads pointed toward the oscillating light and also moving promptly to the positive end of the aquarium. They appear to orient to and also to move toward the source of illumination more promptly than was the case with respect to the stationary light of a similar intensity. Before reaching the positive end of the aquarium, their path becomes oblique to the longitudinal axis of the vessel, this being due, apparently, to the oscillations of the light. On nearing the lighter end of the aquarium, there appears to be some "indecision" as to their direction of movement. There are some attempts to follow the swinging light, but, in the main, many of them make only slight changes in position, after reaching this end of the vessel. Some remain practically stationary, in so far as locomotion is concerned, being engaged in cleaning responses. Others move close to the glass end of the aquarium and attempt both to orient to and also to follow the light.

The responses of water-striders to an oscillating electric light of approximately 22 ca. m. in the field of experimentation, in general, are very similar to those described in the experiments when the stronger light was employed. Twenty gerrids were used in the experiments. Their responses to the source of illumination are positive, but there is neither quite the same promptness in orienting to, nor in moving toward the light as was the case in the experimental work with the light of greater intensity. After nearing the positive end of the aquarium, while their responses are much the same as in the former experiments, with the electric light of stronger illumination, yet in general the responses are rather less definite and precise.

A number of experiments were conducted with a moving, but non-oscillating, electric light of 44 ca. m. in the experimental field. Forty gerrids were used in the experiments and they readily move around the aquarium in which they are confined, in response to a moving light. They either follow just behind the light or else retain positions almost parallel to it. However, these positions vary, for there is not much regularity about this phase of their responses. They readily follow the light, whether it is moved around the aquarium from left to right, or vice versa. If the light is moved about above the gerrids, they tend to keep in the illuminated region. They display much promptness in their responses to the moving light and these apparently are always positive.

The gerrids respond to a moving electric light of half the intensity of the one recently mentioned. Their behavior is very similar to that described when the source of illumination is 44 ca. m. The chief difference is that the responses are not quite so prompt as in the case with the light of greater intensity.

3. Conclusion.

It is evident that responses to contact and to photic stimulation play an important rôle in the daily lives of these water-striders. Such responses appear to form very definite elements in their general behavior. Many of the normal habitat activities, undoubtedly, are due to the thigmotactic and phototactic propensities of these animals. If such forms of stimulation were eliminated from their environment, the result would be a marked modification in the whole general behavior of the species. It is not improbable that the responses of *Gerris remigis* to contact and to light stimuli may have had some influence on the development of certain of the phases of behavior discussed in this paper, perhaps in a manner somewhat analogous to that pointed out by Holmes (1903) in his discussion of the relation of thigmotaxis to the evolution of the death-feigning instinct.

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VI. BIBLIOGRAPHY.

Cole, L. J. 1907. An Experimental Study of the Image-Forming Powers of Various Types of Eyes. *Proc. Amer. Acad. Arts and Sci.*, Vol. XLII, pp. 335-417.

Comstock, J. H., and Comstock, A. B. 1895. *A Manual of the Study of Insects.* (4th ed.; Ithaca, New York: Comstock Publishing Co., 1901). Pp. x + 701; pl. 1; figs. 797.

Essenberg, C. 1915. The Habits and Natural History of the Backswimmers Notonectidæ. *Jour. Animal Behavior*, Vol. V, pp. 381-390.

1915a. The Habits of the Water-Strider Gerris Remigis [Orba]. *Jour. Animal Behavior*, Vol. V, pp. 397-402.

Holmes, S. J. 1901. Phototaxis in the Amphipoda. *Amer. Jour. Physiol.*, Vol. V, pp. 211-234.

1903. Death-Feigning in Terrestrial Amphipods. *Biol. Bull.*, Vol. IV, pp. 191-196.

1905. The Reactions of Ranatra to Light. *Jour. Comp. Neurol. and Psychol.*, Vol. XV, pp. 305-349.

1906. Death-Feigning in Ranatra. *Jour. Comp. Neurol. and Psychol.*, Vol. XV, pp. 200-216.

1907. Observations on the Young of Ranatra Quadridentata Stal. *Biol. Bull.*, Vol. XII, pp. 158-164.

Hungerford, H. B. 1919. *The Biology and Ecology of Aquatic and Semiaquatic Hemiptera.* Bull. Univ. of Kan., Vol. XXI; Sci. Bull., Vol. XI, pp. 1-328; pls. 33.

Jennings, H. S. 1904. *Contributions to the Study of the Behavior of Lower Organisms.* (Publication No. 16; Washington, D. C.: Carnegie Institution.) Pp. 256; figs. 81.

1906. *Behavior of the Lower Organisms.* (Reprinted; New York: Columbia University Press, 1915). Pp. xiv + 366; figs. 144.

Kellogg, V. L. 1908. *American Insects.* (2d ed., revised; New York: Henry Holt and Co.) Pp. xiv + 694; pls. 13; figs. 812.

KIRKALDY, G. W. 1899. A Guide to the Study of British Waterbugs (Aquatic Rhynchota). *Entomologist*, Vol. XXXII, pp. 108-115.

1899a. A Guide to the Study of British Waterbugs (Aquatic Rhynchota). *Entomologist*, Vol. XXXII, pp. 151-154.

MAST, S. O. 1911. *Light and the Behavior of Organisms.* (New York: John Wiley and Sons). Pp. xi + 410; figs. 35.

McCOOK, H. C. 1907. *Nature's Craftsmen: Popular Studies of Ants and Other Insects.* (New York: Harper and Bros.) Pp. xii + 317; pl. 1, figs. 103.

PARSHLEY, H. M. 1917. Insects in Ocean Drift. I. Hemiptera-Heteroptera. *Can. Entom.*, Vol. XLIX, pp. 45-48.

PEARL, R. 1903. The Movements and Reactions of Fresh-water Planarians: a Study in Animal Behavior. *Quar. Jour. Micros. Sci.*, Vol. XLVI, pp. 509-714.

RILEY, C. F. C. 1912. Observations on the Ecology of Dragon-Fly Nymphs: Reactions to Light and Contact. *Ann. Entom. Soc. Amer.*, Vol. V, pp. 273-292.

1919. Some Habitat Responses of the Large Water-Strider, Gerris Remigis Say. *Amer. Nat.*, Vol. LIII, pp. 394-414.

1919a. Some Habitat Responses of the Large Water-Strider, Gerris Remigis Say. II. *Amer. Nat.*, Vol. LIII, pp. 483-505.

1920. Some Habitat Responses of the Large Water-Strider, Gerris Remigis Say. III. *Amer. Nat.*, Vol. LIV, pp. 68-83.

1920a. Migratory Responses of Water-Striders During Severe Droughts. *Bull. Brooklyn Entom. Soc.*, Vol. XV, pp. 1-10.

SEVERIN, H. H. P., AND SEVERIN, H. C. 1911. *An Experimental Study of the Death-Feigning of Belostoma (=Zaitha Aucct.) flumineum Say and Nepa apiculata Uhler.* (Cambridge, Mass.: Henry Holt and Co.) Behavior Monographs, Vol. I, No. 3, pp. 47; pl. 1.

1911a. Habits of Belostoma (=Zaitha) flumineum Say and Nepa apiculata Uhler, with Observations on other Closely Related Aquatic Hemiptera. *Jour. New York Entom. Soc.*, Vol. XIX, pp. 99-108.

DE LA TORRE-BUENO, J. R. 1911. The Gerrids of the Atlantic States (Subfamily Gerrinæ). *Trans. Amer. Entom. Soc.*, Vol. XXXVII, pp. 243-252.

1914. Phototropism in Heteroptera. *Bull. Brooklyn Entom. Soc.*, Vol. IX, pp. 90-96.

1917. Life-History and Habits of the Larger Waterstrider, Gerris Remigis Say (Hem.). *Entom. News*, Vol. XXVIII, pp. 201-208.

1917a. Life History and Habits of the Margined Water Strider, Gerris marginatus Say (Hem., Het.). *Entom. News*, Vol. XXVIII, pp. 295-301.

1920. Remarks on Heteroptera in Beach Drift. *Bull. Brooklyn Entom. Soc.*, Vol. XV, pp. 142-145.

UHLER, P. R. 1884. *The Standard Natural History*, Vol. II. (Edited by J. S. Kingsley; Boston: S. E. Cassino and Co.) Order VI.—Hemiptera, pp. 204-296; pl. 1, figs. 55.

WEISS, H. B. 1914. Notes on the Positive Hydrotropism of *Gerris Marginatus* Say and *Dineutes Assimilis* Aube. *Can. Entom.*, Vol. XLVI, pp. 33-34.